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REVIEWS

Studies of Thermophilic Microorganisms at the Institute of Microbiology, Russian Academy of Sciences

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The thermophily studies at the Institute of Microbiology (INMI), Russian Academy of Sciences, were started more than six decades back, at the end of the 1930s and in the early 1940s. The first experiments to study the metabolic diversity of thermophiles and their physiology, biochemistry, and enzymology were conducted at the institute by A.A. Imshenetskii and his coworkers L.I. Solntseva, S.Z. Brotskaya, and L.A. Kuzyurina. The obtained experimental evidence relating to cellulolytic, amylolytic, and proteolytic thermophiles and their enzymes was generalized in Imshenetskii's monograph *Microbiological Processes at High Temperatures* [1]. This book also compared thermophilic and mesophilic processes and discussed the origin of thermophiles. In 1950, the contemporary view of thermophily was presented in E.N. Mishustin's monograph *Thermophilic Organisms in Nature and Practice* [2], which dealt not only with general and specific properties of thermophilic organisms but also considered their habitats and possible applications. Unlike metabolic diversity, the phylogeny of thermophiles did not figure prominently in any of these monographs, and the experiments and conclusions regarding adaptation of mesophilic species to high temperatures should be regarded as a tribute to the ideology prevailing at the time. Dealing with thermophiles in natural environments, the book focused on soil and anthropogenic biotopes (compost, silage, and self-heating substrates) and on the gastrointestinal tract of higher organisms. The pioneering paper on the microbiology of volcanic habitats was published by S.I. Kuznetsov and was based on his studies of Kamchatka hot springs [3]. The conclusions of this paper outlined all major lines of investigations of thermophilic prokaryotes in their natural habitats that a few decades later were being conducted at the Institute of Microbiology. In the work of Kuznetsov, hyperthermophilic prokaryotes growing at temperatures over 90°C were found and thermophilic microorganisms were shown to be functional in the reductive and oxidative parts of the sulfur cycle and to be involved in mineral formation processes in hot springs.

Studies of thermophilic organisms at INMI in the succeeding years were not only continued but also significantly extended. In the 1960s and 1970s, they were mostly conducted at the Laboratory of Physiology and Biochemistry of Thermophilic Organisms, headed by L.G. Loginova. The results formed the basis of several monographs published in that period [4–6]. Research in the same direction was also carried out in other INMI laboratories, most often in connection with studies of particular environments or processes, such as high-temperature oil fields, studied at Kuznetsov's department, or leaching of sulfide minerals, investigated at the department headed by G.I. Karavaiko. In the 1980s and 1990s, thermophilic microbial communities featured prominently in the research conducted at the Department of Lithotrophic Microorganisms, led by G.A. Zavarzin. An offshoot of this department, the Laboratory of Hyperthermophilic Microbial Communities under E.A. Bonch-Osmolovskaya, was established a few years later. An important event in this field was the All-Union Conference on Thermophilic Microorganisms: Theory and Applications, held in 1983, where more than 30 oral and poster presentations were made by researchers affiliated with INMI [7].

It can be concluded that all subsequent investigations of thermophilic microorganisms at INMI were focused on the basic issues first addressed in the 1940s and 1950s: biological diversity, ecology and biogeochemical activities, physiology and metabolism, and applied aspects.

BIOLOGICAL DIVERSITY OF THERMOPHILIC PROKARYOTES

Investigations of the diversity of thermophilic prokaryotes at INMI were started in the 1970s by Loginova and her coworkers L.A. Egorova, R.S. Golovacheva, G.I. Khraptsova, T.I. Bogdanova, and others. The extremely thermophilic aerobic organotrophic bacterium *Thermus flavus* [8] and a new species, *Thermus ruber* [9], were isolated from Kamchatka hot springs. *T. ruber* was used as an example object in studies of the peculiar morphology of the representatives of this bacterial group, which can form, in the exponential phase, tangles of cells with a common outer membrane

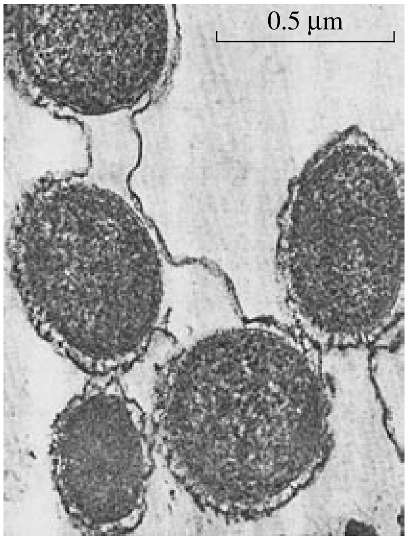


Fig. 1. Thin section of *Thermus ruber* cell aggregates.

(Fig. 1) [10]. Unlike other previously known species of this genus, *T. ruber* grows optimally at 60°C rather than 70–75°C and is, therefore, a moderate thermophile. This species was eventually transferred to the new genus *Meiothermus* of the family *Thermaceae* [11]. The diversity studies of this group of microorganisms at INMI received a surprising continuation almost 30 years later, when representatives of two new genera of the family *Thermaceae*, *Oceanithermus profundus* and *Vulcanithermus mediatlanticus*, were isolated by M.L. Miroshnichenko from deep-sea hydrothermal vents in the Pacific and Atlantic oceans [12, 13]. Like the representatives of the genus *Meiothermus*, the new microorganisms are moderate thermophiles, and, like all *Thermaceae*, they can carry out dissimilatory nitrate reduction with the formation of nitrite. The distinctive feature of these deep-sea species is their microaerophily, previously unknown for *Thermaceae.*

Spore-forming aerobic thermophilic microorganisms were isolated at INMI as producers of different enzymes, mostly hydrolytic, and also in connection with their capacity to utilize saturated hydrocarbons. These organisms were isolated both from anthropogenic biocenoses and high-temperature oil fields [14–16]. The thermophilic bacilli were later assigned to a new genus, *Geobacillus*, proposed by T.N. Nazina *et al.* [17].

The natural habitats of thermophilic prokaryotes in regions of modern volcanism are characterized by the inflow of reduced inorganic compounds, which can serve as substrates for lithoautotrophic prokaryotes. An aerobic hydrogen-oxidizing bacterium *Calderobacterium hydrogenophilum* was isolated from Kamchatka hot springs by V.R. Kryukov *et al.* [18]. The new organism turned out to be an extreme thermophile with a growth optimum at 74–78°C and an obligate autotroph able to grow only on mineral medium in an atmosphere of H_2–O_2–CO_2 (7 : 2 : 1). *Calderobacterium* was later shown to represent the ancient phylogenetic branch *Aquificales*, which consists of only thermophilic prokaryotes, both lithoautotrophic and organotrophic [19]. The capacity for microaerophilic growth with molecular hydrogen was noted for the previously mentioned new deep-sea species of the family *Thermaceae* [12, 13] and for the new microaerophilic organism *Caminibacter profundus*, also isolated from deep-sea hot vents [20].

Reduced sulfur compounds constitute another possible inorganic source of energy for thermophilic prokaryotes. In volcanic habitats, they are represented by hypogene hydrogen sulfide and products of its incomplete oxidation. In ore deposits and dumps, where the temperature can be as high as 60°C, sulfur and sulfide minerals can serve as the energy substrates for microorganisms. The group of lithoautotrophic thermophilic prokaryotes has been explored for many years in Karavaiko's laboratory, and a very important contribution to biodiversity studies was made by Golovacheva [21], particularly by describing the new genus and species *Sulfobacillus thermosulfidooxidans* [22, 23]. This spore-forming aerobic bacterium with an optimal temperature for growth of 50–55°C and a pH optimum of 1.9–2.4 can oxidize elemental sulfur, reduced iron, and a wide range of sulfides. It inhabits hydrothermal vents and self-heated zones in sulfide and sulfur ore deposits. Quite recently, one more species of the same genus, *Sulfobacillus sibiricus*, was described [24]. Golovacheva also isolated a thermophilic iron-reducing bacterium of the genus *Leptospirillum* [25] and thermoacidophilic archaea oxidizing sulfur compounds and assigned to the new species and genus *Sulfurococcus mirabilis* [26].

A thermophilic bacterium that develops in hot springs and oxidizes dissolved volcanic hydrogen sulfide to form white "ostrich feathers" of deposited sulfur was first described by Kuznetsov as *"Thiospirillum pistiense"* [3]. This organism is widespread in volcanic habitats with a temperature of 70–75°C, and its pure culture, isolated much later from hydrothermal vents in Yellowstone National Park, was named *Thermothrix thiopara* [27]. One more species of the same genus, *Thermothrix azorensis*, was isolated by E.V. Odintsova from hydrothermal vents of the Azores [28].

The 1970s were marked by increased interest in anaerobic organisms and by the development at INMI of anaerobic cultivation techniques [29]. Anaerobic thermophiles, like aerobic ones, were found to include organisms that differed widely in terms of their metabolism and belonged to different phylogenetic groups. Several research teams at INMI isolated organotrophic prokaryotes with fermentative metabolism, representing new species and genera of bacteria and archaea. Thus, three species of the genus *Thermoanaerobacter—T. lactoethylicus* [30], *T. sulfurophilus* [31], and *T. siderophilus* [32]—were isolated from Kamchatka hydrothermal vents by V.V. Krivenko, Bonch-

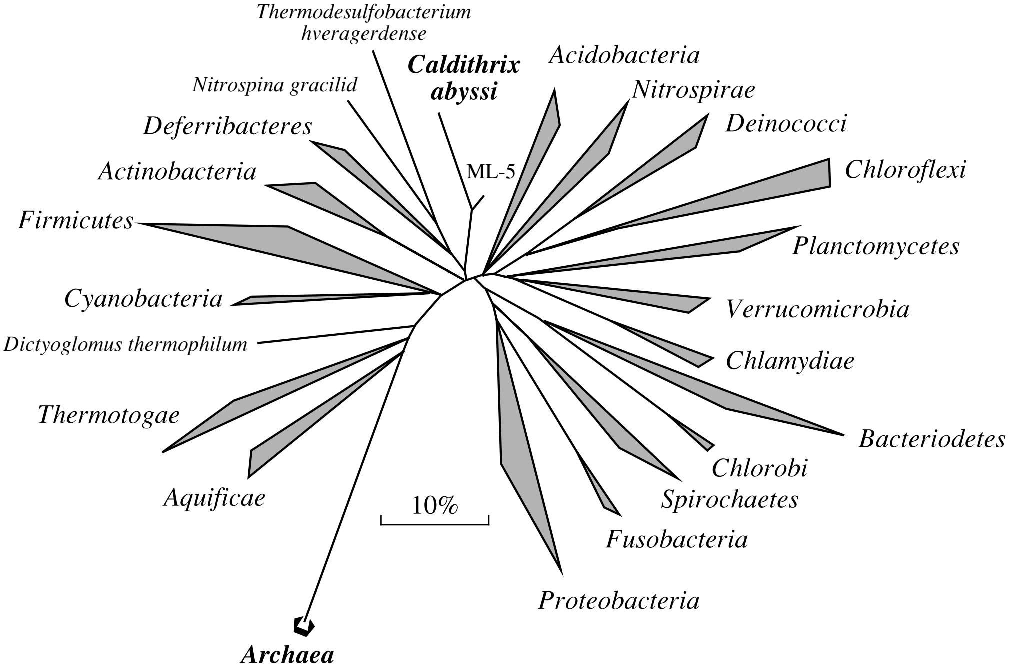


Fig. 2. Phylogenetic position of *Caldithrix abyssi.*

Osmolovskaya, and A.I. Slobodkin. From the same sources, V.A. Svetlichny isolated a new species of anaerobic organotrophic thermophilic bacteria, *Dictyoglomus turgidum* [33], and an isolate with a high cellulolytic activity, which was referred to the new genus and species *"Anaerocellum thermophilum"* [34] but should have probably been assigned to the genus *Caldocellulosiruptor* [35]. Two more anaerobic organotrophic isolates from Kamchatka were obtained by D.G. Zavarzina: the new species *Thermoanaerovibrio velox* [36] and the new genus and species *Thermovenabulum ferriorganovorum* [37]. Representatives of the new species *Thermosipho geolei* [38] were isolated by Miroshnichenko from the high-temperature Samotlor oil field in West Siberia. The new species *Marinitoga piezophila* [39] and a representative of the new species and genus *Tepidibacter thalassicus* [40], which can actively hydrolyze protein, were isolated from deep-sea hydrothermal vents of the East Pacific Rise by Miroshnichenko and Slobodkin. V.M. Gorlenko and collaborators discovered a new anaerobic organotrophic alkalithermophilic species, *Anaerobranca californiensis* [41], in sediments of Mono Lake, California.

All these organisms are gram-positive bacteria, moderately thermophilic, with the temperature optimum in the range of 50–60°C; they are obligate anaerobes with fermentative metabolism. Growth of many of the new organisms is fostered by the presence in the medium of sulfur or iron, serving as inorganic electron acceptors. The capacity to reduce these electron acceptors was found with many thermophilic organotrophs [42, 43]. The ability to reduce nitrate so far appears to be much less widespread. Among the obligately anaerobic organotrophic thermophilic prokaryotes described at INMI, it was found in just one organism, *Caldithrix abyssi*, a new moderately thermophilic bacterium isolated by Miroshnichenko from deep-sea hydrothermal vents of the Mid-Atlantic Ridge [44]. This organism represents a deep-rooted phylogenetic branch in the *Bacteria* domain (Fig. 2) and can grow both organotrophically, by fermenting peptides, and lithotrophically, by utilizing molecular hydrogen and reducing nitrate to ammonium.

Organotrophic anaerobic hyperthermophilic archaea found by Bonch-Osmolovskaya and Miroshnichenko in various thermal habitats, both terrestrial and marine, were classified as the new species *Desulfurococcus amylolyticus* [45], *Thermoproteus uzoniensis* [46], *Thermococcus stetteri* [47], *Thermococcus gorgonarius* (Fig. 3), and *Thermococcus pacificus* [48]. A new species, *Thermococcus sibiricus*, was isolated by Miroshnichenko from formation water of the Samotlor oil field [49]. All these organisms are neutrophilic and differ in this respect from the representative of a new genus and species *Acidilobus aceticus*, isolated by M.I. Prokof'eva, which is an anaerobic thermoacidophile growing optimally at pH 3.8 [50]. All these microorganisms grow at temperatures of 80–90°C; ferment peptides; and, in certain cases, can hydrolyze starch or protein. Most of them are stimulated by the presence of sulfur, which they reduce to hydrogen sulfide.

The diversity of anaerobic lithotrophic prokaryotes turned out to be richer than even that of organotrophs [43]. The energy substrates and electron acceptors they use for growth are both of volcanic origin. New

Fig. 3. Whole cells of *Thermococcus gorgonarius*, negatively stained with phosphotungstic acid.

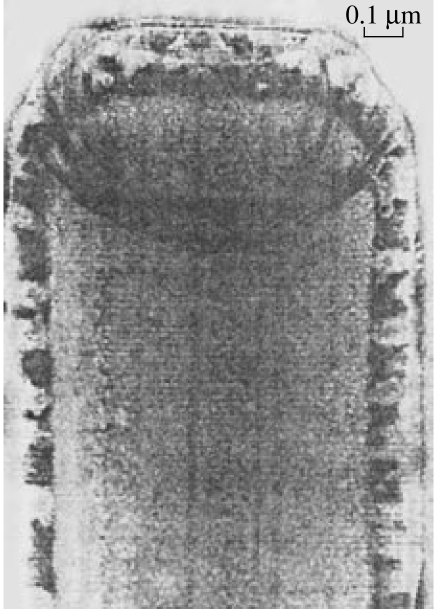


Fig. 4. Whole cells of *Methanothrix* (=*Methanosaeta*) *thermoacetophila*, negatively stained with phosphotungstic acid.

lithotrophs of virtually all physiological groups have been isolated at INMI since 1980. A new species *Methanobacterium thermoformicicum* producing methane from formate was isolated by T.N. Zhilina from an installation for thermophilic manure fermentation [51]. From a cyanobacterial mat in Kamchatka, A.N. Nozhevnikova and T.G. Yagodina isolated a culture of the thermophilic aceticlastic methanogen *Methanothrix thermophila* [52], currently reclassified as *Methanosaeta thermophila* [53]. This organism has a very peculiar cell envelope structure (Fig. 4) [54]. It remains the only aceticlastic methanogen isolated from natural thermal environments. All other thermophilic representatives of the genus *Methanosarcina* were discovered only in anthropogenic biotopes, such as thermophilic methane tanks [55]. Also, no methanogens utilizing single-carbon compounds have been found so far in natural thermophilic communities. As shown by Zhilina and S.A. Ilarionov, the utilization of methanol by a thermophilic culture *"Methanobacillus kuznetsovii"* [56] was actually the result of simultaneous growth of two microorganisms—an acetogen and a methanogen [57, 58].

Thermophilic sulfate-reducing bacteria were isolated from samples obtained from high-temperature oil fields. In 1974, E.P. Rozanova and A.I. Khudyakova described *Desulfovibrio thermophilus* [59], which was later reclassified as *Thermodesulfobacterium thermophilum* [60]. It is a moderately thermophilic bacterium able to reduce sulfate by utilizing lactate and molecular hydrogen. Another moderately thermophilic sulfate-reducing bacterium *Desulfotomaculum kuznetsovii* [61], isolated from underground thermal waters by T.N. Nazina *et al.*, can utilize an exceptionally broad range of substrates, including volatile fatty acids. Finally, a new species of thermophilic sulfate-reducing bacteria *Desulfacinum subterraneum* [62] was recently isolated by Rozanova from a similar biocenosis.

The ability to reduce sulfur is widespread among thermophilic prokaryotes [42]. In addition to the previously mentioned organotrophs able to reduce sulfur in the process of fermentation, there is a wide diversity of microorganisms with the so-called sulfur respiration, which consists in oxidation of nonfermentable substrates by means of elemental sulfur reduction. These are the representatives of new genera *Desulfurella acetivorans* [63], *Desulfurella kamchatkensis* [64], *Desulfurella propionica* [64], and *Hippea maritima* [65], described by Bonch-Osmolovskaya and Miroshnichenko. They occur in terrestrial and marine hydrothermal vents; oxidize volatile fatty acids; alcohols, and saturated fatty acids and can also grow lithotrophically with hydrogen and elemental sulfur. This group of organisms constitutes a separate phylogenetic branch in the kingdom *Bacteria*. The representatives of the new order *Nautiliales*, recently proposed by Miroshnichenko [20] and belonging to the subclass *Epsilonproteobacteria* (Fig. 5), differ from the described organisms in that they can grow only lithotrophically with molecular hydrogen. This order at present consists of two genera represented by three species. *Nautilia lithotrophica* [66] can reduce only elemental sulfur, whereas the species of the genus *Caminibacter* [67, 20] can also reduce nitrate and grow microaerophilically. The ability to reduce elemental sulfur and nitrate was also found in another lithoautotrophic deep-sea isolate *Deferribacter abyssi* [68], which, in addition, can reduce iron.

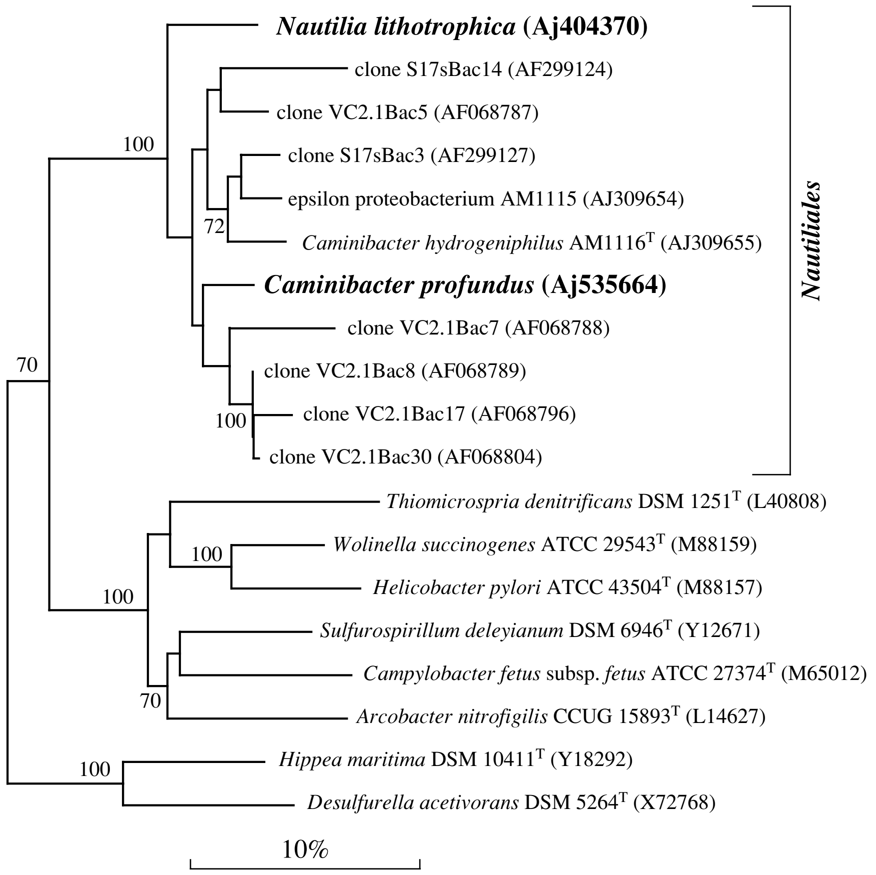


Fig. 5. Phylogenetic position of the order *Nautiliales* within the class *Proteobacteria.*

Apart from molecular hydrogen, volcanic gases contain CO. In the early 1990s, the first thermophilic microorganism able to grow on a mineral medium in an atmosphere composed entirely of CO was isolated by V.A. Svetlichny from Kamchatka hot springs. The new organism, *Carboxydothermus hydrogenoformans* [69], oxidized CO to CO_2 anaerobically, forming hydrogen from water (Fig. 6). The morphological diversity of microorganisms observed in thermophilic enrichment cultures exhibiting this reaction suggests its wide occurrence in thermophilic prokaryotes [70]. This was indeed shown to be the case when several pure cultures of new microorganisms, *Carboxydothermus restrictus* [71], *Carboxydobrachium pacificum* [72], *Carboxydocella thermoautotrophica* [73], and *Thermosinus carboxydivorans* [74], were isolated by T.G. Sokolova. These gram-positive microorganisms do not constitute a single phylogenetic group and were isolated from terrestrial and marine hydrothermal vents in different regions of the world. In addition to bacteria that depend obligately on CO (*C. restrictus* and *C. thermoautotrophica*), this reaction can be carried out by microorganisms that grow by means of fermentation (*C. pacificum*) or anaerobic respiration (*T. carboxydivorans*). The ability to grow lithotrophically by oxidizing CO with the concurrent formation of hydrogen from water was also found by Sokolova in a strain of hyperthermophilic archaea of the genus *Thermococcus* isolated from abyssal hydrothermal vents at the East Pacific Rise [75]. The outlined evidence indicates an extremely wide occurrence of this process in thermophilic prokaryotes.

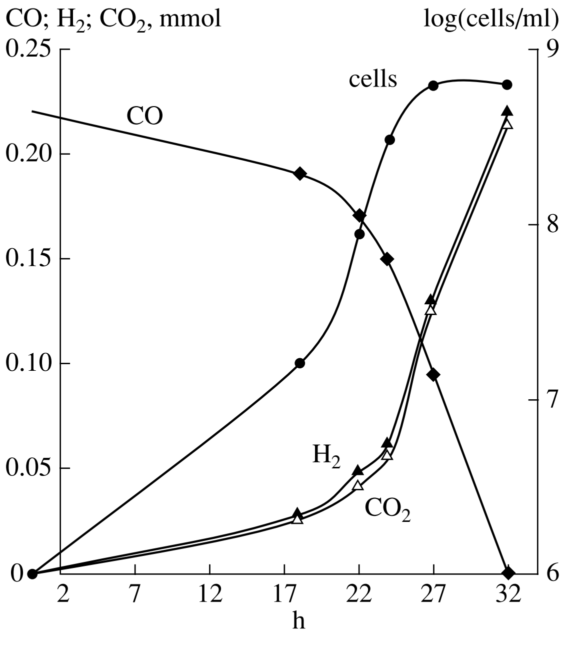


Fig. 6. Growth, utilization of CO, and production of CO_2 and hydrogen by *Carboxydothermus hydrogenoformans.*

More than 60 years of exploration of the biodiversity of thermophilic prokaryotes at INMI resulted in the description of a large number of new taxa: a new order, a new family, 19 new genera, and 43 new species, not to mention two new remote phylogenetic branches the status of which is still to be clarified. The new isolates represent virtually all phylogenetic and physiological groups: they include archaea; gram-positive and gram-negative bacteria; moderate, extreme, and hyperthermophiles; thermoacidophiles and thermoalkaliphiles; aerobes, anaerobes, and microaerophiles; and organotrophs and lithoautotrophs; among them are hydrogen-oxidizing and CO-trophic prokaryotes; methanogens; and sulfate, sulfur, nitrate, and iron reducers.

ECOLOGY AND BIOGEOCHEMICAL ACTIVITIES OF THERMOPHILES

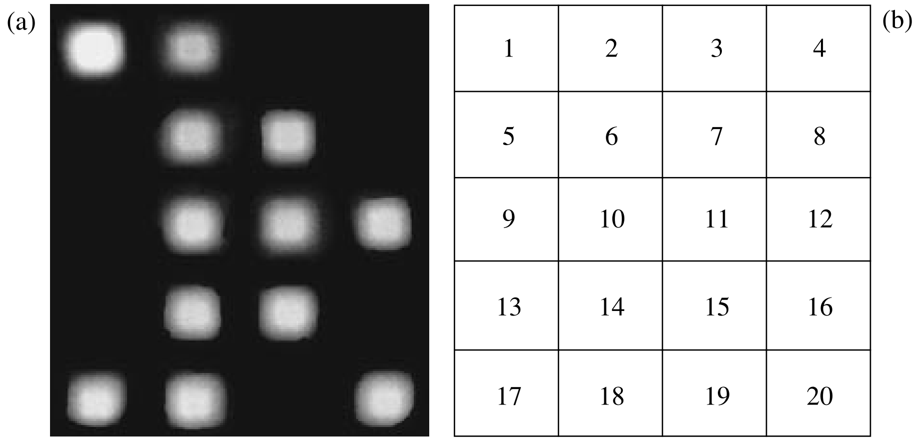
The ecology and biochemical activities of thermophilic prokaryotes attract considerable interest because their communities are thought to represent modern analogues of the early biosphere. The best studied habitat of such organisms is the Uzon caldera in Kamchatka, and the results of its perennial investigation were generalized in the collective monograph *Microorganisms of Calderas* edited by Zavarzin [76]. Several approaches were employed in studies of natural communities of thermophilic prokaryotes. The distribution of a selected genus or physiological group of microorganisms was analyzed; the microbial community species composition in the given habitat was studied; laboratory models were developed to clarify the ecological significance of a certain community component; and radioisotopic methods were used to determine the rates of microbial processes.

Investigations of thermophilic microorganisms in their natural habitats, initiated by Kuznetsov [3], were continued by many INMI researchers. The objects of these studies were physiological or taxonomic groups of microorganisms and their specific habitats. Thus, Loginova and collaborators studied the distribution of the genus *Thermus* in hot springs of Kamchatka, the Kurils, and Tajikistan [77]. The composition and the distribution of thermophilic cyanobacteria were studied by L.M. Gerasimenko and collaborators using as an example cyanobacterial mats in the Uzon caldera and on Kunashir Island [78]. Gorlenko and collaborators determined the species composition and population number of phototrophic bacteria in hot springs of Lenkoran, the Uzon caldera, the Lake Baikal coast, and the Barguzin River valley [79–81]. The species diversity was found to decrease rapidly at elevated temperatures, and, at temperatures above 60°C, the sole predominant species was *Chloroflexus aurantiacus.* The thermophilic bacteria with sulfur respiration were shown by Bonch-Osmolovskaya's group to proliferate in sediment and bacterial accretions depositing in terrestrial and shallow-water marine hydrothermal vents [82]. The same group also studied the occurrence of lithoautotrophic thermophilic prokaryotes in Kamchatka hot springs with different physicochemical conditions [83] and the distribution of thermophilic prokaryotes in formation water of a high-temperature oil reservoir [84]. In addition to cultural methods, the latter study employed a biological microchip with oligonucleotide probes specific to 16S rRNA of different genera or groups of genera of thermophilic prokaryotes (Fig. 7).

Several molecular biology–based approaches to identification of thermophilic prokaryotes of different phylogenetic groups were developed by N.A. Chernyh, A.V. Lebedinsky, and collaborators [85–87] and used in studies of the distribution of thermophilic prokaryotes in terrestrial and marine habitats. A hyperthermophilic archaeon of the genus *Sulfophobococcus* was recently first found in a thermophilic anaerobic digestor of a wastewater treatment station near Moscow [88].

The ecological role of thermophilic prokaryotes was studied using laboratory models of their natural communities. V.V. Balashova simulated a thermophilic sulfureta, where thiosulfate was reduced in the anaerobic zone and the generated hydrogen sulfide was oxidized to elemental sulfur in the aerobic zone [89]. The structure and functions of thermophilic cyanobacterial mats were also reproduced in laboratory simulations by V.K. Orleanskii [90]. Gerasimenko and Zavarzin studied the influence of a cyanobacterial mat on the composition of a mixture simulating volcanic gases and showed their transformation into a modern oxygen-containing atmosphere (Fig. 8) [91, 92].

The processes in thermal environments were studied for a number of years in several INMI laboratories by using radioisotopic methods. The rate of primary organic matter production by means of oxygenic and anoxygenic photosynthesis was determined by Gorlenko and collaborators in cyanobacterial mats of the Uzon caldera [93] and hot springs of the Baikal region [81]. The rate of primary production in a community associated with *Thermothrix* was found to be surprisingly low, suggesting a lithoheterotrophic type of metabolism in this organism [93]. The assimilation of organic carbon in shallow-water hydrothermal vents in the western Pacific was studied by B.B. Namsaraev and collaborators during the 18th voyage of the research vessel *Academik Nesmeyanov* in 1990 [94]. In hot springs of the Uzon caldera with temperatures of 60, 70, and 80°C and pH 3.5, 7.0, and 8.5, the primary production was detected by N.V. Pimenov and I.I. Rusanov only at 60 and 80°C, which can be explained by the activity of lithoautotrophic moderately thermophilic bacteria and thermophilic archaea [83]. The decomposition of organic matter in natural communities of thermophilic prokaryotes is known to proceed at different rates and its terminal process is determined by the availability of electron acceptors. The rates of lithotrophic and aceticlastic methanogenesis in high-temperature oil fields of China and West Siberia were measured by Nazina *et al.* [95, 96, 84]. The predomi-



1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16
17	18	19	20

Fig. 7. Use of a biological microchip to determine the distribution of thermophilic prokaryotes in the formation waters of the Samotlor oil field: (a) Results of hybridization of oligonucleotide probes with the PCR product obtained with 16S rDNA–targeted universal primers on the native DNA isolated from formation water occurring at the depth of 2384 m; (b) arrangement of oligonucleotide probes on the microchip: (1) *Thermotoga–Thermosipho*; (2) *Geotoga*; (3, 4) *Petrotoga*; (5) *Methanobacterium* spp.; (6) *Methanothermobacter* spp.; (7) all *Methanobacterium* and *Methanothermobacter*; (8) empty gel element; (9) *Thermodesulfobacterium*; (10) *Thermoanaerobacter*; (11) *Thermococcus* and *Pyrococcus*; (12) *Thermococcus*; (13) *Desulfurococcus*; (14) *Desulfotomaculum* (except for *D. ruminis* and *D. nigrificans*); (15) *D. ruminis* and *D. nigrificans*; (16) empty gel element; (17) *Thermus*; (18) *Aquificales* + *Desulfurobacterium* + *Thermovibrio*; (19) empty gel element; (20) *Geobacillus.*

nant process—sulfate reduction or methanogenesis—was shown to be determined by the presence of sulfates in the formation water. High-temperature sulfate reduction and methanogenesis, including aceticlastic, were also shown to proceed in samples from Jurassic horizons with the temperature of 84°C. This fact suggests that deep-subsurface habitats are populated by indigenous microflora that includes until now unknown groups of microorganisms. By employing radioisotopic methods, the major processes of anaerobic destruction proceeding in shallow-water hydrothermal vents of the west Pacific were characterized [94]. The organic matter destruction in these habitats was found to proceed at a significant rate and terminate with methane production and sulfate or sulfur reduction [94, 97]. The source of sulfur is its short cycle operating in the tidal zone. Similar cycles can be effective in bacterial accretions found in terrestrial hot springs, where hydrogen sulfide formed in the course of sulfate or sulfur reduction is oxidized by phototrophic or aerobic lithoheterotrophic community members [98]. In low-sulfide hot springs, the organic matter of cyanobacterial mats, synthesized in the course of oxygenic or anoxygenic photosynthesis, is decomposed with the production of methane or hydrogen sulfide as the terminal reduced product [99].

Ecological investigations of natural thermal habitats undertaken by different research groups employing different approaches showed closed carbon and energy cycles to be functional in these systems. The organic matter can be of autochthonous (cyanobacterial mats and high-temperature hot springs) or allochthonous origin, supplied with meteoric waters by means of thermal convection [100]. Different types of anaerobic respiration can play the leading role in anaerobic destruction, and it is the metabolic diversity of thermophilic prokaryotes that makes the cycles of biogenic elements complete in such habitats.

PHYSIOLOGICAL AND BIOCHEMICAL STUDIES OF THERMOPHILIC PROKARYOTES

Many of the pure cultures of thermophilic prokaryotes isolated at INMI were used in physiological and biochemical studies. Thus, an extremely thermophilic aerobic hydrogen-oxidizing bacterium *Calderobacterium hydrogenophilum* and a hyperthermophilic archaeon *Thermococcus stetteri* were used as objects in the hydrogenase activity studies conducted by M.A. Pusheva [18, 101]. Both enzymes exhibited strong activities at high temperatures and a high thermal stability. The discovery of hydrogenase activity in *T. stetteri* first seemed at odds with the absence of hydrogen utilization or production by this organism. However, by studying its growth as a function of the gas phase volume, Bonch-Osmolovskaya and Miroshnichenko were able to show that, at low concentrations of hydrogen, it is indeed produced as a sole reduced product of fermentation [102]. The inhibiting effect of hydrogen is responsible for the fact that many fermentative thermophiles depend facultatively or obligately on the presence of elemental sulfur or iron [31, 103, 104]. As shown by Slobodkin, many of these organisms are able to grow lithoheterotrophically by reducing ferric oxide with molecular hydrogen [105]. However, lithoautotrophic iron reduction was shown only for *Thermoterrabacterium ferrireducens*, possessing a CO dehydrogenase [104].

An exceptionally high thermal stability of the CO dehydrogenase was shown in an anaerobic CO-oxidizing bacterium *Carboxydothermus hydrogenoformans* by Pusheva and Sokolova [106]. The assimilation of carbon dioxide in another lithoautotrophic thermophilic organism—an aerobic hydrogen bacterium *Pseudomonas thermophila*—was studied in detail by A.K. Romanova and E.E. Emnova [107]. Somewhat later, ribulose 1,5-bisphosphate carboxylase was isolated from the cells of this organism and characterized [108].

Thermophilic archaea and bacteria were also used as objects in studies of the processes responsible for the transport of carbohydrates and amino acids into the cell. I.A. Usenko conducted such studies for the cells of *Thermococcus stetteri*, *Pyrococcus furiosus, Desulfurococcus amylolyticus*, and *"Anaerocellum thermophilum"* [109].

Despite the pioneering nature of many of the physiological and biochemical investigations of thermophilic prokaryotes undertaken at INMI, such studies remained, admittedly, more or less sporadic. For example, there were virtually no attempts to completely characterize the metabolism of new isolates, and interest was focused mostly on the key enzymes of catabolic metabolism. As regards anabolic processes, most of the papers were devoted to enzymes involved in autotrophic growth. Both lines of research are closely connected with the understanding of the functioning of natural microbial communities and, in this respect, continue directly the ecophysiological approach that was predominant at INMI over recent decades. A significant part of physiological and biochemical studies was instigated by practical applications of thermophilic microorganisms.

STUDIES OF THERMOPHILIC MICROORGANISMS FOR BIOTECHNOLOGICAL APPLICATIONS

The biotechnological applications of thermophilic microorganisms are mostly connected with the exceptional stability of their hydrolytic enzymes. Such enzymes can be used to advantage in detergent production and in the food and cellulose industries. Active studies of thermophilic and thermotolerant cellulose- and xylanase-producing strains of the fungi *Aspergillus terreus* and *Myceliophthora thermophila* were undertaken in Loginova's laboratory [110–113]. In particular, the hydrolytic enzymes of *M. thermophila* were found to be very active in the temperature range from 25 to 80°C, with an optimum at 65°C [114]. The studies of this strain were later continued in the laboratory headed by E.P. Feofilova [115, 116].

Loginova's collaborators selected thermophilic bacteria and actinomycetes (*Bacillus circulans* and *Actinomyces vulgaris*) producing alpha-amylase with a temperature activity peak at 75°C [117]. Studies of alpha-amylase biosynthesis in *Bacillus stearothermophilus* [118] showed increased amylase activity in continuous cultures of this organism. Studies of the protease biosynthesis by thermophilic actinomycetes were also conducted and an inventor's certificate was obtained for the strain *Thermoactinomyces vulgaris* INMI-4a, producing serine thiol-dependent protease with lytic properties [119]. This strain was later also shown to produce a metal-containing protease (carboxypeptidase); the variation of enzymatic activities caused by the original strain splitting into clones as a result of natural variability was studied [120]. A potential application of enzymatic preparations obtained from *Thermoactinomyces vulgaris* INMI-4a for casein hydrolysis in the production of nutrient media for microorganisms and for hydrolysis of serum protein was analyzed [121, 122].

Another possible use of thermophilic microorganisms lies in agricultural waste treatment to produce ethanol or methanol. In this connection, anaerobic thermophilic cellulolytic bacteria determined as *Clostridium thermocellum* and forming ethanol as one of the main products of cellulose decomposition were isolated from hot springs in Buryatia [123]. To produce ethanol from cellulose, a mixed association of thermophilic bacteria was used with the capacity to accumulate in the medium up to 1.3% ethanol in the course of growth on cellulose [124]. The generation of methane from livestock breeding wastes by thermophilic associations of microorganisms was studied by Nozhevnikova *et al.* [55], and the temperature optimum of the process was found to be close to 52°C. At the same time, the process rate was found to increase significantly compared to that of spontaneous manure fermentation by natural microflora upon the addition of a preadapted inoculum with a methanogen content several orders of magnitude higher than that in manure. The methanogens were mostly constituted by the aceticlastic species *Methanosarcina mazei* and *Methanothrix (Methanosaeta) thermophila.* The inoculum was enriched with aceticlastic methanogens by adding to manure additional amounts of acetate.

In connection with the vigorous development of molecular biology and genetic research methods in recent decades, thermophilic microorganisms were applied in the production of thermostable enzymes of nucleic acid metabolism and, above all, DNA polymerases. A screening conducted at the Laboratory of Hyperthermophilic Microbial Communities revealed that many hyperthermophilic archaea possess thermostable high-fidelity DNA polymerases [125].

CONCLUSIONS

It is worth noting in conclusion that the exploration of thermophilic prokaryotes, started at INMI more than 60 years ago, never stopped and goes on today. Virtually all INMI laboratories and departments participated in this research, looking into different aspects of the biology of thermophilic organisms. Different research directions prevailed at different periods, but the general trend consisted in passing from the physiology and biochemistry of individual organisms to the community structure revealed through studies of the diversity of thermophilic prokaryotes and the range of biogeochemical processes they carry out. It would be reasonable to suppose that, after some time, the researchers will once again turn to studies of the physiology and metabolism of thermophiles and this will give new depth to investigations of thermophilic microbial communities.

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